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RESEARCH ARTICLE

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Index of host habitat preference explored by movement-based simulations and trap captures

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Abstract

1. Animal species likely have different strengths of host habitat preference (HHP) that might be characterized by a standardized index ranging from 0 (no preference) to 1 (maximum preference). We hypothesized that in some species, HHP may result from individuals dispersing out of the host habitat having a probability of turning back at the boundary, or after entering host habitat by reducing speed or increasing size of turning angles.
2. Computer simulations of individuals moving between various sized patches of host and nonhost habitat were conducted based on these three behaviours hypothesized to affect HHP.
3. In the rebounding model, simulations resulted in equilibria of animal numbers inside and outside of host habitat that depend on sizes of these areas, initial number and the rebounding probability. Curvilinear regression of simulation results suggested an equation that predicted numbers in the host habitat and was solved for rebounding probability. A modified equation that sampled population densities (e.g., insect pheromone trap catches) inside and outside host habitat areas gave the rebounding probability, an index of HHP, without requiring the sizes of the areas. Simulations with traps and moving animals verified that the modified equation could predict the index correctly. The modified equation also estimates an index of HHP from sampled densities due to speed reductions and a combination of this and rebounding. Changes in angular turning size upon entering host habitat, however, did not affect habitat preference.
4. Using pheromone trap captures, we found that the lesser date moth *Batrachedra amydraula* has a HHP for date *Phoenix dactylifera* plantations of 0.96. Host habitat preference indexes also were calculated from sampled insect densities reported in the literature.
5. The new index of HHP is useful to characterize habitat patches of many organisms and aid understanding of animal spatial distributions and speciation processes. In addition, the index can be applied in studies of invasive species, trap crops of pest insects and conservation management.

KEYWORDS
Batrachedra amydraula, computer simulation model, date palm, host preference, insect sampling, landscape ecology, pheromone, population ecology

1 | INTRODUCTION

Host habitat selection has been defined by Jaenike and Holt (1991) “as any behaviour that causes an individual to experience a set of environmental states different from that expected to be encountered by individuals moving at the same rate randomly through the environment.” Host habitat selection has also been called host habitat location (Quilici & Rousse, 2012; Vet, 1983) or host habitat preference (HHP; Eitam & Vargas, 2007; Segura et al., 2016). Some authors refer merely to habitat selection or choice, habitat preference or host habitat (Cotes et al., 2015; de Meeus, Hochberg, & Renaud, 1995; Nosil, Crespi, Sandoval, & Kirkpatrick, 2006; Rausher, 1984; Zhao & Kang, 2002), and may or may not want to differentiate between hosts and habitat. Some species are mainly found on the host animal or plant while other species are commonly found in surrounding habitat and only briefly on the host. Agricultural regions often consist of several crops of monoculture plant species each fed upon by several herbivorous insect species (Kuno, 1991) having various ill-defined host plant preferences. Host habitats are intimately associated with the concept of patches in spatial and landscape ecology (Hunter, 2002; Pickett & Cadenasso, 1995).

Boyce and McDonald (1999) proposed using resource selection functions to map habitat use probability, and the sum of these probabilities would indicate population abundance (Boyce et al., 2016). Movement-based models of habitat choice such as step-selection functions and resource selection functions have been developed for larger vertebrates that can be followed by GPS biotelemetry or by visual observations (Avgar, Potts, Lewis, & Boyce, 2016; Boyce et al., 2016; Gillies & St. Clair, 2010; Mason & Fortin, 2017; Patterson, Thomas, Wilcox, Ovaskainen, & Matthiopoulos, 2007; Thurfjell, Ciuti, & Boyce, 2014). In contrast, insects are small and essentially invisible in flight, thus their relative abundance, movements and spatial distributions can only be readily studied with traps that intercept or attract (Byers, 1999, 2012a, 2012b; Byers & Naranjo, 2014; Landolt & Phillips, 1997), or by conventional sampling methods (Kuno, 1991). In this study, we are mainly concerned with insect herbivores that are well known to have high affinities for specific host plants in agricultural or forestry systems (e.g., Byers, 1989; Knolhoff & Heckel, 2014; Landolt & Phillips, 1997; Levi–Zada et al., 2013; Zehnder & Trumble, 1984). However, our approach presented below can be applied to any mobile animal exhibiting patch habitat preference, such as caribou (Mason & Fortin, 2017). Hereafter, we refer to HHP as an ecological factor in which visual, tactile and olfactory cues aid the species in remaining relatively longer within a habitat containing their host plants.

Knowledge of the magnitude of HHP appears important to understanding speciation processes because a mutation in host preference can lead to individuals having feeding preference for a secondary host plant species in the same or another location that reduces genetic mixing (Berlocher & Feder, 2002; Johnson, Hoppensteadt, Smith, & Bush, 1996; Nosil, Sandoval, & Crespi, 2006; Rausher, 1984; Webster, Galindo, Grahame, & Butlin, 2012). Over many generations, the mating isolation of populations in different host habitats in conjunction with both genetic drift and natural selection can lead to a second species on the secondary host plant. The extent of HHP for each population and the geographic distance will impact the time for speciation to occur. A mosaic of habitat patches delineated by HHP may indicate the potential of an invasive species to infest new regions due to increasing global commerce and climate changes (Hulme, 2009).

Many insect species show a high degree of host plant specificity and thus some degree of HHP (Berlocher & Feder, 2002; Knolhoff & Heckel, 2014; Landolt & Phillips, 1997). Female moths (Lepidoptera) seek mates and sites on host plants to lay eggs while males seek calling females releasing pheromone in these areas (El-Sayed, Knight, Byers, Judd, & Suckling, 2016). Bark beetles (Coleoptera: Curculionidae) are another example in which both sexes seek forest trees that are often in stands of nearly one species, for example, Norway spruce or Scots pine in Europe interspersed by meadows or deciduous trees (Byers, 1989; Byers, Lanne, Löfqvist, Schlyter, & Bergström, 1985). Lygus plant bugs (Miridae) disperse from less preferred cotton hosts to the preferred host alfalfa (Bancroft, 2005). Olfactory mechanisms appear to aid moths, bark beetles, parasitoid wasps and many other insects in finding and staying in host habitat by means of attraction to pheromones and host plant volatiles (Byers, 1989; Byers et al., 1985; Cotes et al., 2015; El-Sayed et al., 2008, 2016; Landolt & Phillips, 1997; Quilici & Rousse, 2012; Vet, 1983; Zhao & Kang, 2002). Many insects appear to have evolved behaviour to search in a random forward direction for host habitats until finding appropriate odour of host plants or insects (Byers, 1989, 1991, 1999, 2012a, 2012b; Levi–Zada et al., 2018).

Here, we attempt to calculate an index for the magnitude of HHP based on an animal's movement behaviour that results in different densities in the respective areas. One behaviour that would engender HHP would be where an animal turns back into the host habitat area at its boundary by means of visual and olfactory cues. For example, Schultz and Crone (2001) observed that a prairie butterfly changed directions within 10–22 m after leaving host habitat. This is analogous to an attraction to host habitat over a few metres. In our model, it does not matter if the rebounding movement (attraction) occurs some metres before or after leaving the boundary. This border-rebounding behaviour resulting in HHP would have a probability, the highest being 1 in which the animal always rebounds into the host habitat interior, while at the other extreme, a probability of 0 would not affect the movement of the organism as it passed from the host habitat across the boundary to the outside. We assume an insect that flies into its host habitat would not change its flight direction regardless of its innate HHP. We expect that monophagous insects feeding on one host plant species would have high host habitat affinity and an index of HHP near 1, while a polyphagous herbivore would have lower HHP for an agricultural crop adjacent to less preferred crops.

Our first goal was to develop simulations whereby animals inside host habitat that attempted to leave would turn back inside with a probability equal to HHP. We expected equilibrium populations to result regardless of initial distributions based on the relative sizes of host habitat and outside areas as well as the strength of the HHP. Based on simulation results, we wanted an equation that predicted numbers inside host habitat and could be solved for HHP. After the initial simulations provided insights into the process, a second equation was desired that could yield HHP based only on densities inside and outside the host habitat. This equation was found and simulations of moving insects captured by circular traps verified that HHP could be calculated simply from the sampled population densities inside and outside host habitat without knowledge of their spatial sizes. We hypothesized that the lesser date moth *Batrachedra amydraula* Meyrick (Lepidoptera: Batrachedridae) that feeds on fruits of date palms (*Phoenix dactylifera* L.) would exhibit a strong HHP for date palm plantations that are usually surrounded by desert areas. We estimated population densities of *B. amydraula* by pheromone trap catches inside and outside of a date palm plantation and used them with the last mentioned equation to estimate HHP of the moth in date plantations. Effects on HHP of reducing the step size of movement or increasing the range of turning angles while inside host habitat also were explored. Lastly, we demonstrate using simulations that our HHP approach can be extended to vertebrates sampled sequentially by position through time.

2 | MATERIALS AND METHODS

2.1 | Simulation of animals entering and leaving host habitat areas

Animal movement was simulated in two dimensions within an *x*- and *y*-coordinate system of 300 × 300 m. One thousand points, for example representing flying insects, began moving in the area according to a correlated random walk for each individual (Byers, 2012a, 2012b). Each insect point was given an initial position and angle θ_0 at random and then moved in 0.5 m steps (*s*), with each step from x_0, y_0 to x_1, y_1 calculated as a polar vector from the former direction and position using the formulas: $x_1 = x_0 + s \cdot \cos(\theta_1)$ and $y_1 = y_0 + s \cdot \sin(\theta_1)$, where $\theta_1 = \theta_0 + \alpha$ in which α is an angle chosen at random from a normal distribution with standard deviation (*SD*) = 4°. If an insect tries to move outside the boundaries of the simulation area, then it rebounds at a random angle that allows movement back into the area (Byers, 1991).

At each step, the insect travels a straight line that can be calculated to intersect any of several line segments forming a polygon to determine whether the insect passes into or out of a centrally placed polygon representing the host habitat (Manber, 1989, p. 267). If the insect's step would pass from inside to outside the polygon, then if a uniform random number from 0 to <1 is greater than the specified probability of HHP (e.g., 0.8), then the insect is allowed to leave, otherwise it rebounds at a random angle back into the polygon's interior and then continues initially in the rebounding direction in a correlated random walk. This movement can be described as a rebounding behaviour when attempting to move out of the host habitat. When insects pass into the host habitat area, there is no effect on their path. In most simulations, the polygon of host habitat was a square of 100 × 100 m placed centrally within the larger simulation area.

The simulations above allowed insects to fly in the area for 14,400 steps (7,200 m), a distance sufficient to reach equilibrium, in which the HHP probability inside the central square area was varied from 0 to 1 in increments of 0.05 (*N* = eight simulations each). At the end of each simulation, numbers of insects found within the host habitat or outside this area were recorded. Simulations with different relative sizes of the host habitat and outside areas, or placement of host habitat in the corner or centrally in the larger simulation area, were conducted to explore the density relationships after equilibrium. The simulations were performed in the Java language (Java 1.6.06; Oracle, Redwood Shores, CA) on a personal computer. Diagrams and graphs were programmed with PostScript language (Adobe Systems Inc., San Jose, CA).

2.2 | Fitting regression functions to simulations

A formula was desired that would predict the number inside the host habitat area based on (a) sizes of host habitat area and outside area, (b) the initial number of animals in the entire area and (c) the HHP. An HHP = 0 means that there is no preference and insects freely pass in and out of the host habitat area. In this case, the number predicted within the host habitat (N_i) would simply be the total number (N_T) multiplied by the proportion of the inner host habitat area (A_i) of the total area (A_T). Thus, for N_T = 1,000 insects and A_i = 10,000 and A_T = 90,000 m^2, there should be about N_i = 111 insects within the A_i at all times during the simulation. However, N_i would vary as a Poisson variable due to random movements. At the other extreme, an HHP = 1 means that all insects eventually enter and remain in the inner host habitat area (N_i = 1,000). The problem is to find N_i at other values of HHP. Data generated by the simulations were fit by least squares regression to a large number of functions by TableCurve 2D version 5.01 (Systat Software Inc., Chicago, IL). The function with the best fit (highest R^2) might give insights into an equation that would calculate N_i and could be solved for HHP given numbers in the two areas after equilibrium.

2.3 | Equations predicting HHP from sampling by trap catches or tracked positions

Assuming an equation could be found that uses the five variables: N_i, N_T, A_i, A_T and HHP then any of these could be solved for, although N_i and especially HHP would be the variables of most interest. It was also conceptualized that the numbers inside (N_i) and outside (N_o) the host habitat area divided by areas A_i and ($A_T - A_i$), respectively, are densities that could be reflected by trap catches in the corresponding areas. Similar to that, densities of large vertebrates would be reflected in the numbers of GPS recordings over an extended period in corresponding areas of equal size. Using the equation derived in the previous section (presented in Section 3) and trap captures, it was

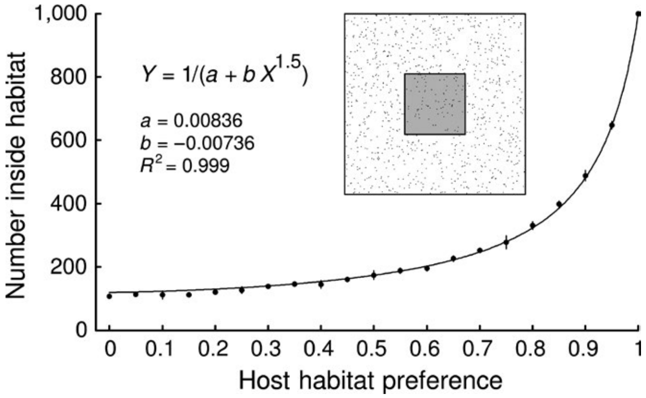

FIGURE 1 Number of simulated insects inside the inner host habitat area (100 × 100 m shaded square) as a function of host habitat preference (HHP). Simulations (n = 8 each point, ±95% CI) based on 1,000 insects each flying for 14,400 steps (each 0.5 m) in a 300 × 300 m area. The regression equation was fitted by TableCurve 2D software

desired that a formula be derived that would predict HHP. This equation was found and simplified, and P (or HHP) was found according to a range of mean trap catches inside (C_i) and outside (C_o) the host habitat. A regression equation was also fit to this plot.

Simulations were performed to verify the equations by methods similar to those above but by placing from 1 to 4 traps within A_i and the same number outside A_i after equilibrium affected by a given HHP had occurred (traps were placed beginning after 7,200 steps of simulation). Each trap was assumed to have a semiochemical, such as a pheromone, that had a circular effective attraction radius (EAR_c) of 0.5 m that is reasonable for insects (Byers, 2012a). The EAR_c intercepts all insects that strike the circle (Byers, 2012b). However, the EAR_c size is not critical as the ratios of catch inside and outside host habitat area are what determine HHP, as will be shown subsequently. The pheromone traps were placed at random within A_i as well as outside of A_i, but with no overlap of EAR_c among traps. Insects entering or moving through any trap's EAR_c were caught as determined by a geometric algorithm (Byers, 1991). In other simulations (N = 8), 20 vertebrates were tracked by position beginning after 7,200 steps at HHP = 0.95. The position of each vertebrate was noted every 100 steps and recorded as being inside host habitat or in an equal area outside the host habitat (N = 72 positions per animal). The value of C_i was set to the number of recordings inside host habitat, while C_o was equal to the number of recordings in the outside area for use in the HHP equation using trap catches above.

The HHP for male lesser date moth *B. amydraula* in a 315 × 350 m date palm plantation (*P. dactylifera*) surrounded by desert was determined by sampling population density inside and outside the host habitat. The date palms were 10–17 m in height and planted in a grid of 9 m spacing between trees. Each of four delta pheromone traps baited with 1 mg of active sex pheromone components (Levi–Zada et al., 2011, 2013, 2018) was placed 25 m diagonally from each corner inside the date orchard located in the Arava Valley, Israel (29°56′31″N, 35°4′42″E). An additional four traps were placed 100 m and four traps 200 m outside the plantation in the desert. Mean catches were calculated after 2 weeks (22 August–5 September 2016) and used to calculate HHP from Equation (5) in Section 3. Simulations with model parameters above were used to explore variability of trap catches corresponding to those in the date plantation (Section 3) as well as variation in calculated HHP.

2.4 | Effects of changes in movement behaviour

Another behaviour besides rebounding was envisioned that could explain or contribute to HHP. Instead of an insect turning back at the border of the host habitat area according to a specific probability, the insect could merely move slower (or spend more time on host plants before flying to another) while inside the host habitat compared to outside. These simulations without rebounding behaviour caused insects upon entering the habitat area to take much smaller steps (either 0.05, 0.075, ... 0.475 m in 0.025 increments) than while outside the area where steps were 0.5 m. Trapping inside and outside the host habitat area, as described above, was also simulated with varying step lengths. Numbers inside the host habitat or P calculated from Equation (3) in Section 3 that resulted from simulations with different step sizes were fit to curvilinear functions as above. Various two-way combinations in which step size was varied from 0.5 to 0.025 m in 0.025 m increments and HHP from 0 to 1 in 0.05 increments when inside the host habitat were also simulated (N = 4 each combination, other parameters as above). The numbers resulting inside the host habitat, or calculated P, were fit to surface equations (TableCurve 3D version 3.01, Systat).

Another algorithm that might achieve a HHP allows the insect to make larger random turns at each step only when inside host habitat area. This could happen when insects moved between host plants at random. Thus, the 4° *SD* of turning angles used outside the host habitat was changed to 120° upon entering the host habitat, causing a highly circuitous, Brownian motion-like movement.

3 | RESULTS

3.1 | Simulation of animals entering and leaving host habitat areas

The numbers of animals or insects found inside the host habitat area after each individual took correlated random walks of 14,400 steps (0.5 m each) depend on the rebounding probability at the host habitat boundary (Figure 1). The numbers inside host habitat after equilibrium resulted showed a gradual increase that begins to accelerate "geometrically" as the HHP increases above 0.5 (Figure 1). The numbers inside host habitat (N_i) after equilibrium also depend on the host habitat area (A_i) relative to the entire area (A_T). For example, at HHP = 0, we found that N_i depends on the number of insects distributed initially at random throughout the entire area (N_T) as well as the proportion that A_i is of the entire area A_T. However, when HHP = 1, then all animals given enough time ended up in the host habitat area

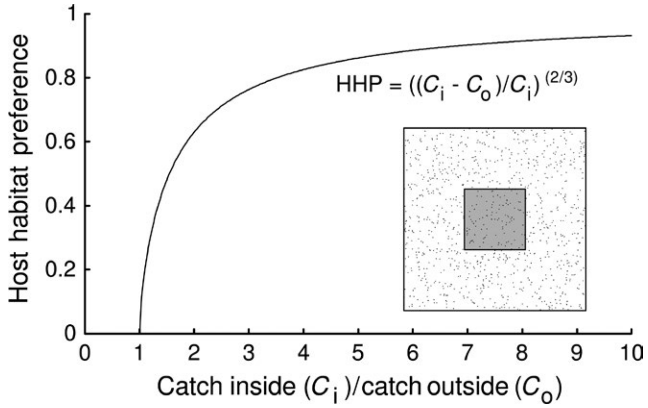

FIGURE 2 Host habitat preference (HHP) as a function of the ratio of mean catch inside habitat (C_i, shaded inner square) to mean catch in outside habitat (C_o). The equation was simplified from Equation (4) and used to generate the curve of HHP for the shaded area

no matter what the relative size of the host habitat area was to the total area.

3.2 | Fitting regression functions to simulations

The fitting of regression functions to the simulated data (Figure 1) indicated that the number inside (N_i) was fitted well (adjusted R^2 = 0.9987) with the following function:

$$N_i = \frac{1}{a + b \cdot P^{1.5}} \quad (1)$$

where a = 0.00836, b = −0.00736, and P is HHP. Using the given areas (A_i = 10,000; A_T = 90,000) and N_T = 1,000, the coefficients a and b have values that are close to $A_T/(N_T \cdot A_i)$ = 0.009 and $(A_i - A_T)/(N_T \cdot A_i)$ = −0.008 so these were substituted into Equation (1):

$$N_i = \frac{1}{(A_T/(N_T \cdot A_i)) + ((A_i - A_T)/(N_T \cdot A_i)) \cdot P^{1.5}} \quad (2)$$

Thus, from Equation (2) if P (or HHP) = 0.62, and A_T, A_i and N_T are as above, then N_i = 196.29 while from Equation (1) then N_i = 209.8. Equation (2) with P = 0.93 predicts N_i = 547.9 or with Equation (1) then N_i = 568.5, and both equations predict N_i = 1,000 at P = 1. Other simulations with different relative sizes of host habitat and outside areas gave the same relationship as in Equation (1), and although coefficients a and b were different values than above they agreed with values given by the ratios in the denominator of Equation (2). Equation (2) can be solved for P:

$$P = \left[\frac{N_T \cdot A_i - N_i \cdot A_T}{N_i \cdot A_i - N_i \cdot A_T}\right]^{2/3} \quad (3)$$

Thus, the HHP or P above can be found from four parameters above. The magnitude of step size or *SD* of turning angle distribution, assumed constant throughout areas, only affected the time to reach equilibrium and not the resulting population densities at equilibrium.

3.3 | Equations predicting HHP from sampling by trap catches or tracked positions

Equation (3) would be difficult to use in practice because N_T and N_i are very difficult to observe in the field, however, they can be approximated by the respective densities obtained from a ratio of trap catches inside and outside the host habitat. It will be shown, in fact, that the areas A_T and A_i surprisingly have no effect on P, which makes it possible to easily evaluate HHP in nature. This would be carried out by placing one to several traps inside the host habitat area and similar numbers of traps outside this area. The trap catches would reflect the densities (numbers per area) in the host habitat and outside this area. If we let C_i be the average catch inside the host habitat area, and C_o be the average catch outside the host habitat area, then N_T is proportional to $C_i \cdot A_i + C_o \cdot (A_T - A_i)$ and N_i is proportional to $C_i \cdot A_i$. We can then substitute the catch formulas for N_T and N_i into Equation (3) and obtain the following:

$$P = \left[\frac{C_i \cdot A_i + C_o \cdot (A_T - A_i) \cdot A_i - C_i \cdot A_i \cdot A_T}{C_i \cdot A_i \cdot A_i - C_i \cdot A_i \cdot A_T}\right]^{2/3} \quad (4)$$

Equation (4) gives the same results for P as Equation (3) but it was found that both equations do not depend on the sizes of areas A_i and A_T. However, Equation (2) that calculates N_i does depend on the sizes of these areas. Using Equation (4), with the above parameters, if average C_i = 12.8 and C_o = 2.4 ($C_o \le C_i$) then P = 0.87. However, changing A_i to 30,000 with A_T = 90,000 as above does not affect P. This was initially surprising but Equation (4) can be simplified to:

$$P = \left[\frac{C_i - C_o}{C_i}\right]^{2/3} \quad (5)$$

The terms A_i and A_T drop out in Equation (5) indicating they are not relevant since P remains at 0.87. Using either Equation (4) or (5), a curved relationship is revealed between the ratio of mean catches inside and outside the host habitat (C_i/C_o) and P (Figure 2).

Simulations of several traps inside the host habitat area with various HHP and several traps outside the host habitat gave mean catches inside (C_i) and outside (C_o) that were used in Equation (5) to calculate P, which was similar in all cases to the HHP set in the simulations (Table 1). These results confirm that Equation (5) is valid and that HHP is simple to calculate from field trap catches using semiochemicals. This calculation works as long as the inside catch mean is greater than the outside catch mean, which is expected as host habitat area should have a higher density of insects than does nonhabitat area. The simulated GPS tracking of vertebrates with HHP = 0.95 gave mean numbers of successive recordings inside host habitat (C_i = 923.9 ± 41.9) or in an equal area outside of host habitat (C_o = 63.5 ± 15.3) that were used in Equation 5 to yield a mean HHP = 0.953 ± 0.012 (±95% CI, N = 8).

TABLE 1 Resulting *P* of host habitat preference after simulations with various numbers of traps with mean catch inside host habitat (C_i) of area A_i and catch outside (C_o) in the larger total area (A_T) given different host habitat preferences (HHP). Resulting catches in simulations were used to calculate a host habitat preference (*P*) from Equation (4) or Equation (5) where both formulas give the same result

Insects	Traps[a]	C_i	C_o	A_i	A_T	HHP	*P*
1,000	3	64.5 ± 5.7[b]	30.7 ± 2.7[b]	10,000	90,000	0.62	0.64 ± 0.06[b]
1,000	3	48.7 ± 2.4	24.6 ± 2.0	40,000	90,000	0.62	0.62 ± 0.03
1,000	1	50.6 ± 6.5	25.9 ± 4.0	40,000	90,000	0.62	0.61 ± 0.07
1,000	4	47.0 ± 3.3	22.2 ± 1.9	40,000	90,000	0.62	0.65 ± 0.04
1,000	3	91.8 ± 5.2	43.9 ± 5.1	22,500	40,000	0.62	0.64 ± 0.05
1,000	3	109.8 ± 2.1	17.0 ± 2.4	22,500	40,000	0.90	0.89 ± 0.02
500	3	55.9 ± 4.4	10.5 ± 3.0	22,500	40,000	0.90	0.87 ± 0.05
1,000	3	45.8 ± 2.0	35.1 ± 3.5	10,000	90,000	0.30	0.36 ± 0.12
500	3	102.6 ± 2.7	9.3 ± 1.1	2,500	90,000	0.95	0.94 ± 0.01

[a]Trap EAR_c of 0.5 m, 4 hr of 0.5 m steps s^{-1} with traps deployed after 7,200 steps when equilibrium had been reached; host habitat area placed in centre of larger area.
[b]Values ±95% CI (*N* = 8 simulations).

This result supports the use of GPS tracking data to calculate HHP.

Equation 5 was used with the catches of male lesser date moths on traps inside a date plantation (mean 14.5 ± 2.6, *N* = 4) and 100–200 m outside the plantation (mean 0.88 ± 0.69, *N* = 8) to give an HHP = 0.96. To estimate 95% confidence limits for the HHP of this month, eight simulations with 95 insects (Table 1 parameters, four traps each area) gave mean catches inside and outside host habitat of 14.41 ± 0.93 and 0.97 ± 0.34, respectively, giving HHP of 0.95 ± 0.02. These simulated catches and resulting confidence interval are similar and not significantly different from the natural mean catches or the calculated HHP of 0.96.

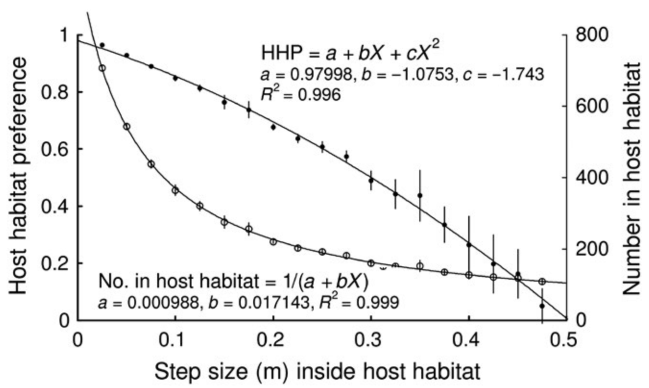

FIGURE 3 Host habitat preference and number of insects inside host habitat as a function of step size inside host habitat. Step size was 0.5 m outside host habitat; parameters as in Figure 1 but without rebounding probability; error bars 95% CI. The host habitat preference was calculated from Equation (3)

3.4 | Effects of changes in movement behaviour

Changes in step size (*s*) when entering host habitat area affected the densities within and outside the host habitat area and thus the HHP. The number of animals accumulating in the host habitat area increased in an inverse function with a decrease in step size upon entering the area (Figure 3). Using Equation (3) and the numbers in the respective areas resulted in a linear-like quadratic function in which HHP increased with a decrease in step size inside the host habitat (Figure 3). However, trapping with semiochemicals did not yield HHP as in the border-rebounding model as catches inside and outside the host habitat remained the same regardless of step size. For example, at s = 0.05 inside host habitat and s = 0.5 outside, the mean catches of three traps were similar at 19.2 ± 2.5 (±95% CL, *N* = 8) inside and 19.5 ± 2.1 outside. When s = 0.5 in both areas, then catches were higher but also similar, 32.9 ± 3.0 inside and 35.3 ± 1.8 outside. Thus, *P* calculated from trap catches was approximately 0 regardless of step size. Although catches on traps inside and outside were about the same, usually the catches inside of host habitat were slightly smaller than outside (e.g., as above).

Combining a higher HHP = 0.9 with smaller step size (s = 0.1 m) inside the host habitat produced an even stronger build-up of insects (825.6 ± 6.5, *N* = 8) than either effect alone (485.1 ± 14.1 or 375.8 ± 12.2, respectively). The combined effect concomitantly increased HHP to 0.98 ± 0.001. A combination of HHP = 0.8 with step size 0.1 m gave means of 705.4 ± 10.7 and HHP of 0.96 ± 0.002. The numbers of insects (*Z*) inside the host habitat (or corresponding calculated HHP) increased as a result of varying HHP from 0 to 1 (*X*) and step size from 0.025 to 0.5 (*Y*) inside the host habitat, with constant step size of 0.5 m outside this area (Figure 4a,b). The best-fitting simple equation for insect numbers (Figure 4a) was $Z = -55.3 + 560\ X^3 - 203.3\ \ln(Y)$ with $R^2 = 0.98$. However, this and other functions did not fit the data as HHP approached 1.

In simulations in which there was no rebounding behaviour but *SD* of turning angles was changed from 4° to 120° upon entering the host habitat, a circuitous Brownian-like motion resulted in which animals hardly moved any distance over time. However, this type of movement did not cause a build-up of animals inside the host habitat (or at other large *SD*) because the insects that

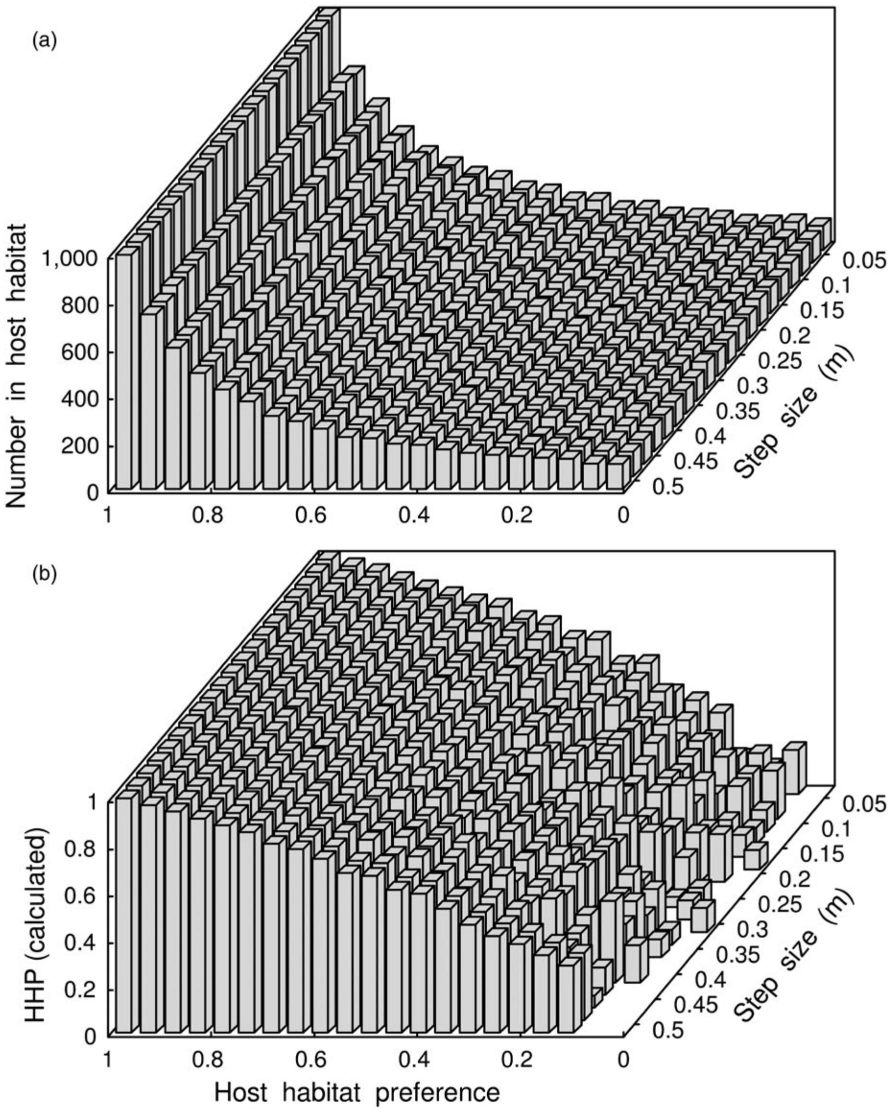

FIGURE 4 (a) Number of insects inside host habitat as a function of host habitat preference (HHP) and step size inside host habitat. Step size was 0.5 m outside host habitat; parameters as in Figure 1. (b) HHP (calculated host habitat preference from Equation 3) as a function of host habitat preference and step size inside host habitat

entered host habitat remained close to the boundaries and soon were likely to leave in the direction of exit (outward to nonhost habitat). The number of insects at 4° *SD* was approximately 111 (proportional to area or 1/9 of 1,000 insects) while this number was about the same at *SD* = 120° (106.9 ± 6.5, *N* = 8). In models that combined HHP = 0.9 with *SD* = 120°, higher numbers built up inside the host habitat (617.0 ± 9.0), especially along the periphery of the host habitat and decreasing towards its centre. However, the mean 617 was significantly higher than the mean at the same HHP but *SD* = 4° (485.1 ± 14.1; or 481 from Figure 1). Thus, there is some effect of turning angle distribution when combined with rebounding values of HHP > 0.

4 | DISCUSSION

The affinities of herbivores for host habitats compared to outside areas would depend primarily on the mixtures and densities of host and nonhost plant species in the respective areas. We assume that in some species, individuals dispersing out of a host habitat area have a specific probability of rebounding inward. In this model, HHP is determined by a ratio of densities in host habitat and outside, which can be estimated by insect captures on pheromone traps. In other species, a combination of behaviours such as reduced speed, increased turning angles and rebounding results in higher densities in host habitat compared to outside that gives an HHP index with Equation (5). This ratio of densities can be estimated by traditional sampling methods.

Turchin (1991) proposed a “residence index” to describe an affinity of a species for particular host habitat. He developed Patlak’s 1953 diffusion equation of random walks so that observed movement data of individuals inside and outside host habitat could be used to calculate a ratio of densities between the two areas. Turchin showed how observed animal movement data (mean move length, mean squared move length, mean move duration and mean cosine of turning angle) recorded in earlier studies would reasonably predict the ratio of observed densities between the host habitat and outside areas. However, it must be noted that the actual densities cannot be predicted as only a ratio is obtained. Turchin's study indicates that different animal movements inside host habitat and outside would lead to an equilibrium of respective densities depending on the initial number of animals, as also found in our simulation results. Turchin (1991) used data (his table 2) taken from Odendaal, Turchin, and Stermitz (1989) on a female butterfly searching for larval host plants that gives a residence index = 0.123 inside the host patch and 0.044 outside (Turchin's eqn 9). The ratio of these values is 2.78 which is close to the ratio of observed densities of 6.09/1.84 = 3.31 (Odendaal et al., 1989; Turchin's table 3). However, applying our Equation (5) with these densities gives HHP = 0.79, so the residence index of Turchin is not the same as our HHP index. Instead we do not use animal movement parameters in our index but merely the observed respective densities to obtain our index.

Animals or insects in our rebounding simulation model turned back when leaving the host habitat area according to a set probability equal to HHP. If the HHP was set at 1, all insects would eventually find and remain within the host habitat. As HHP was increased above zero towards 0.5, the number of insects within the host habitat gradually increased, further increases in HHP caused numbers to grow increasingly rapidly as an inverse power of *P* to a maximum limit at HHP = 1 (Figure 1). This regression relationship (Equation 1) would have different *a* and *b* coefficients if the ratio of inside area (A_i) to total area (A_T) as well as total number (N_T) was different, but Equation (2) would still calculate the correct number inside host habitat (N_i). The numbers inside the host habitat area can be calculated from total area, host habitat area and total animals from Equation (2), and the *P* (or HHP) could be calculated from numbers inside and outside the host habitat and the respective areas from Equation (3). However, these values of N_i and *P* are not possible to calculate in the field as the numbers within each area, and the area outside the host habitat, are not easily defined. In practice, the catches on traps inside and outside (or numbers of GPS recordings inside and outside) the host habitat can be used to reflect the numbers multiplied by the proportions of areas in Equation (4). In a fortunate way, the areas cancel out in Equation (5) and the HHP can be calculated simply from the trap catches (or GPS recordings) inside and outside the host habitat area. Simulations with various numbers of insects and traps in different sizes of host habitat with a given HHP relative to outside areas showed that trap catch can be used to calculate HHP accurately (Table 1).

Host habitat preference could also be affected by changes in movement behaviour such as a reduction in step size (or speed) upon entering the host habitat which caused an increase in numbers therein and a higher HHP (Figure 3). However, trapping with pheromones in simulations of this type did not yield the appropriate HHP because catches were similar on traps inside and outside the host habitat area, giving HHP equal to zero. The reason catch was similar inside and outside the host habitat was that encounter rate models predict that catch is a function of speed and density (Byers, 2012a; Byers & Naranjo, 2014; Levi–Zada et al., 2018). Thus, as speed decreased (smaller steps), a compensatory increase in density occurred as insects remained longer, which caused no differences in catch between the inside and outside areas. The lower mean catch of about 19 at lower speed inside the host habitat was due to an accumulation of insects within the host habitat and consequent lower density in the outside areas (but catches in both areas remained the same). Although catches on traps inside and outside were about the same, usually the catches inside the host habitat were slightly lower than catches outside. This was because the three traps inside the smaller host habitat area competed more for the insects compared to the three traps in the eight times larger outside area. While pheromone baited traps would not help to calculate HHP with insects that exhibited changes in speed after entering host habitat, sampling density with other methods discussed subsequently would give correct HHP. If pheromone trapping methods and area sampling methods gave similar HHP, then the rebounding model is indicated, otherwise if different HHP is estimated then slower speed inside the host habitat is indicated.

A third way that insect behaviour might affect HHP could be if the insects increase turning angles once entering host habitat. However, increasing sizes of turning angles this way without rebounding behaviour did not cause higher densities in host habitat and thus cannot affect calculated HHP. This was because insects that increase turning angle distribution upon entering the host habitat begin to move in more "uncorrelated random walks" similar to Brownian motion. This effectively stops forward progress into the host habitat interior and causes a much higher chance of exiting host habitat as the insect is at the boundary. Any step outward then causes the insect to make larger steps away from the host habitat. The simulations show this behaviour clearly with no build-up of insects in the host habitat at any *SD* of turning angles from 4° to 120°. Turchin (1991) concluded earlier that an increased klinokinesis inside the host habitat will not contribute to spatial redistributions of the population.

Our results with catches of the monophagous lesser date moth on traps baited with sex pheromone inside and outside a date plantation used with Equation (5) gave an HHP = 0.96. In most simulations, a correlated random walk of flight was assumed both inside and outside the host habitat as indicated in several studies of flying insects (Byers, 2012a). This type of flight also was indicated from catches of lesser date moths on traps baited with female-equivalent dispensers (FD) of 10 μg pheromone in a date plantation (Levi–Zada et al., 2018). The FD traps were placed every 9 m for 72 m in four cardinal directions outward from a strong monitoring trap baited with 1 mg pheromone (100 times more than FD dose). The similar catches on the FD traps further than 36 m from the monitoring trap indicated that male moths fly uniformly throughout the palm tree plantation. The 1 mg strong pheromone plume increased catch on FD traps 9 m away from the monitoring trap but this effect became insignificant >18 m away in one plantation and >36 m away in another (Levi–Zada et al., 2018). The male lesser date moths may rebound into date palm host habitat due to a combination of visual and olfactory processes. In a typical manner, orientation behaviour of insects within odour plumes from host plant or pheromone sources occurs over a few tens of metres (as indicated above;

Murlis, Elkinton, & Cardé, 1992; Byers, 1989). It should be noted that Equation (5) is calculated from a ratio of sampled densities between the host habitat and outside areas, this ratio is usually consistent (Boyce et al., 2016). Thus, estimates of HHP are not expected to vary with insect abundance in systems with substantial attraction to host plants. However, insects that are primarily attracted to pheromone of conspecifics in host habitats may show a comparatively higher HHP at higher abundance and density of pheromone sources than when at lower abundance.

Semiochemical traps can appropriately determine HHP for animals with a probability of turning back at the host habitat boundary, but this trapping method would not calculate HHP for animals reducing their speed at the boundary. However, net sweeping of host habitat and outside areas would access population density (using same number sweeps for both types of areas) appropriately for either slower speed or turning back behaviours using Equation (5). Thus, population density estimates (numbers per unit area) from sweep nets, quadrant samples, vacuums or other unit area sampling (Kuno, 1991) can be compared within a host habitat or crop to other nonhost habitats or crop species in areas nearby. For example, Zehnder and Trumble (1984) reported higher densities of the leafminer fly *Liriomyza sativae* on tomato plots compared to that on nearby plots of celery in California. Using their Table 1, the HHP for tomato can be calculated from Equation (5) and ranged from 0.40 to 0.98 (mean 0.75 ± 0.23, ±95% CL). They found another leafminer, *L. trifolii*, preferred celery with HHP calculated to range from 0.83 to 0.99 (0.94 ± 0.06). In pest management, the HHP method should aid in the discovery of appropriate trap crops used to protect an economic crop (Shelton & Badenes–Perez, 2006). For instance, Kloen and Altieri (1990) counted an average density of 204 cabbage aphids *Brevicoryne brassicae* in a trap crop of mustard compared to 3.84 in the protected crop of broccoli, giving HHP = 0.99 for mustard. They found an HHP for peach aphid *Myzus persicae* in mustard of 0.90.

While our focus was on insects, HHP indexes could also be calculated for vertebrates (Mason & Fortin, 2017) if their populations are sampled at random within defined areas inside and outside their host habitat patches. In addition, sequentially sampling positions of vertebrates by GPS or other means over extended periods as animals move between host habitat and an area outside of equal size would give densities, as found in our simulations, that can be used to calculate HHP from Equation (5). However, HHP calculations would likely be more difficult to interpret for vertebrates with complex interactive behaviours over larger scales than for insects. For example, habitat use in polar bears varies with season due to trade-offs between foraging and retreat (Mauritzen et al., 2003), while preferred grassland habitat use by elk varies with presence of wolves (Creel, Winnie, Maxwell, Hamlin, & Creel, 2005). Equation (5) here can be used with multiple patches by simply averaging the sampled densities inside and outside the habitat and nonhabitats. With the HHP index, it is possible to compare many species to easily determine the strengths of their affinities for host habitat in an exact and standardized indexing method.

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AUTHORS' CONTRIBUTIONS

J.A.B. conceived the ideas, conducted simulations, and analysed data; A.L.-Z. and A.S. constructed pheromone traps; A.S. collected field data; J.A.B. and A.L.-Z. led the writing of the manuscript, all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The data on lesser date moth, executable simulation programs (java jar files), and the corresponding java code can be found in the figshare archive https://doi.org/10.6084/m9.figshare.6470927.v1 (Byers, 2018).

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REFERENCES

Avgar, T., Potts, J. R., Lewis, M. A., & Boyce, M. S. (2016). Integrated step selection analysis: Bridging the gap between resource selection and animal movement. *Methods in Ecology & Evolution*, *7*, 619–630. https://doi.org/10.1111/2041-210X.12528

Bancroft, J. S. (2005). Dispersal and abundance of *Lygus hesperus* in field crops. *Environmental Entomology*, *34*, 1517–1523. https://doi.org/10.1603/0046-225X-34.6.1517

Berlocher, S. H., & Feder, J. L. (2002). Sympatric speciation in phytophagous insects: Moving beyond controversy? *Annual Review Entomology*, *47*, 773–815. https://doi.org/10.1146/annurev.ento.47.091201.145312

Boyce, M. S., Johnson, C. J., Merrill, E. H., Nielsen, S. E., Solberg, E. J., & van Moorter, B. (2016). Can habitat selection predict abundance? *Journal of Animal Ecology*, *85*, 11–20. https://doi.org/10.1111/1365-2656.12359

Boyce, M. S., & McDonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*, *14*, 268–272. https://doi.org/10.1016/S0169-5347(99)01593-1

Byers, J. A. (1989). Chemical ecology of bark beetles. *Experientia*, *45*, 271–283. https://doi.org/10.1007/BF01951813

Byers, J. A. (1991). Simulation of mate-finding behaviour of pine shoot beetles, *Tomicus piniperda*. *Animal Behaviour*, *41*, 649–660. https://doi.org/10.1016/S0003-3472(05)80903-0

Byers, J. A. (1999). Effects of attraction radius and flight paths on catch of scolytid beetles dispersing outward through rings of pheromone traps. *Journal of Chemical Ecology*, *25*, 985–1005. https://doi.org/10.1023/A:1020869422943

Byers, J. A. (2012a). Estimating insect flight densities from attractive trap catches and flight height distributions. *Journal of Chemical Ecology*, *38*, 592–601. https://doi.org/10.1007/s10886-012-0116-8

Byers, J. A. (2012b). Modelling female mating success during mass trapping and natural competitive attraction of searching males or females. *Entomologia Experimentalis et Applicata*, *145*, 228–237. https://doi.org/10.1111/eea.12006

Byers, J. (2018). Index of host habitat preference. *figshare*. Fileset. https://doi.org/10.6084/m9.figshare.6470927.v1

Byers, J. A., Lanne, B. S., Löfqvist, J., Schlyter, F., & Bergström, G. (1985). Olfactory recognition of host-tree susceptibility by pine shoot beetles. *Naturwissenschaften*, *72*, 324–326. https://doi.org/10.1007/BF00454776

Byers, J. A., & Naranjo, S. E. (2014). Detection and monitoring of pink bollworm moths and invasive species using insect pheromone traps and encounter rate models. *Journal of Applied Ecology*, *40*, 1041–1049. https://doi.org/10.1111/1365-2664.12270

Cotes, B., Rännbäck, L. M., Björkman, M., Norli, H. R., Meyling, N. V., Rämert, B., & Anderson, P. (2015). Habitat selection of a parasitoid mediated by volatiles informing on host and intraguild predator densities. *Oecologia*, *179*, 151–162. https://doi.org/10.1007/s00442-015-3326-2

Creel, S., Winnie, J. Jr., Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, *86*, 3387–3397. https://doi.org/10.1890/05-0032

deMeeus, T., Hochberg, M. E., & Renaud, F. (1995). Maintenance of two genetic entities by habitat selection. *Evolutionary Ecology*, *9*, 131–138. https://doi.org/10.1007/BF01237752

Eitam, A., & Vargas, R. I. (2007). Host habitat preference of *Fopius arisanus* (Hymenoptera: Braconidae), a parasitoid of tephritid fruit flies. *Annals of the Entomological Society of America*, *100*, 603–608. https://doi.org/10.1603/0013-8746(2007)100[603:HHPOFA]2.0.CO;2

El-Sayed, A. M., Byers, J. A., Manning, L. M., Jürgens, A., Mitchell, V. J., & Suckling, D. M. (2008). Floral scent of Canada thistle and its potential as a generic insect attractant. *Journal of Economic Entomology*, *101*, 720–727. https://doi.org/10.1093/jee/101.3.720

El-Sayed, A. M., Knight, A. L., Byers, J. A., Judd, G. J. R., & Suckling, D. M. (2016). Caterpillar-induced plant volatiles attract conspecific adults in nature. *Scientific Reports*, *6*, 37555, 14 pp. https://doi.org/10.1038/srep37555

Gillies, C. S., & St. Clair, C. C. (2010). Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology*, *47*, 182–190. https://doi.org/10.1111/j.1365-2664.2000.01756.x

Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, *46*, 10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Hunter, M. D. (2002). Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology*, *4*, 159–166. https://doi.org/10.1046/j.1461-9563.2002.00152.x

Jaenike, J., & Holt, R. D. (1991). Genetic variation for habitat preference: Evidence and explanations. *The American Naturalist*, *137*, S67–S90. https://doi.org/10.1086/285140

Johnson, P. A., Hoppensteadt, F. C., Smith, J. J., & Bush, G. L. (1996). Conditions for sympatric speciation: A diploid model incorporating habitat fidelity and non-habitat assortative mating. *Evolutionary Ecology*, *10*, 187–205. https://doi.org/10.1007/BF01241784

Kloen, H., & Altieri, M. A. (1990). Effect of mustard (*Brassica hirta*) as a non-crop plant on competition and insect pests in broccoli (*Brassica oleracea*). *Crop Protection*, *9*, 90–96. https://doi.org/10.1016/0261-2194(90)90084-K

Knolhoff, L. M., & Heckel, D. G. (2014). Behavioral assays for studies of host plant choice and adaptation in herbivorous insects. *Annual Review of Entomology*, *59*, 263–278. https://doi.org/10.1146/annurev-ento-011613-161945

Kuno, E. (1991). Sampling and analysis of insect populations. *Annual Review of Entomology*, *36*, 285–304. https://doi.org/10.1146/annurev.en.36.010191.001441

Landolt, P. J., & Phillips, T. W. (1997). Host plant influences on sex pheromone behavior of phytophagous insects. *Annual Review of Entomology*, *42*, 371–391. https://doi.org/10.1146/annurev.ento.42.1.371

Levi–Zada, A., Fefer, D., Anshelevitch, L., Litovsky, A., Bengtsson, M., Gindin, G., & Soroker, V. (2011). Identification of the sex pheromone of the lesser date moth, *Batrachedra amydraula*, using sequential SPME auto-sampling. *Tetrahedron Letters*, *52*, 4550–4553. https://doi.org/10.1016/j.tetlet.2011.06.091

Levi–Zada, A., Sadowsky, A., Dobrinin, S., David, M., Ticuchinski, T., Fefer, D., … Blumberg, D. (2013). Reevaluation of the sex pheromone of the lesser date moth, *Batrachedra amydraula*, using autosampling SPME-GC/MS and field bioassays. *Chemoecology*, *23*, 13–20. https://doi.org/10.1007/s00049-012-0115-9

Levi–Zada, A., Sadowsky, A., Dobrinin, S., Ticuchinski, T., Fefer, D., Dunkelblum, E., & Byers, J. A. (2018). Pest detection and trapping methodologies demonstrated with lesser date moth *Batrachedra amydraula*. *Bulletin of Entomological Research*, *108*, 58–68. https://doi.org/10.1017/S0007485317000487

Manber, U. (1989). *Introduction to algorithms: A creative approach*. Reading, MA: Addison-Wesley.

Mason, T. H. E., & Fortin, D. (2017). Functional responses in animal movement explain spatial heterogeneity in animal–habitat relationships. *Journal of Animal Ecology*, *86*, 960–971. https://doi.org/10.1111/1365-2656.12682

Mauritzen, M., Belikov, S. E., Boltunov, A. N., Derocher, A. E., Hansen, E., Ims, R. A., … Yoccoz, N. (2003). Functional responses in polar bear habitat selection. *Oikos*, *100*, 112–124. https://doi.org/10.1034/j.1600-0706.2003.12056.x

Murlis, J., Elkinton, J. S., & Cardé, R. T. (1992). Odor plumes and how insects use them. *Annual Review of Entomology*, *37*, 505–532. https://doi.org/10.1146/annurev.en.37.010192.002445

Nosil, P., Crespi, B. J., Sandoval, C. P., & Kirkpatrick, M. (2006). Migration and the genetic covariance between habitat preference and performance. *The American Naturalist*, *167*, E66–E78. https://doi.org/10.1086/499383

Nosil, P., Sandoval, C. P., & Crespi, B. J. (2006). The evolution of host preference in allopatric vs. parapatric populations of *Timema cristinae* walking-sticks. *Journal of Evolutionary Biology*, *19*, 929–942. https://doi.org/10.1111/j.1420-9101.2005.01035.x

Odendaal, F. J., Turchin, P., & Stermitz, F. R. (1989). Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). *Oecologia*, *78*, 283–288. https://doi.org/10.1007/BF00377167

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2007). State–space models of individual animal movement. *Trends in Ecology & Evolution*, *23*, 87–94. https://doi.org/10.1016/j.tree.2007.10.009

Pickett, S. T. A., & Cadenasso, M. L. (1995). Landscape ecology: Spatial heterogeneity in ecological systems. *Science*, *269*, 331–334. https://doi.org/10.1126/science.269.5222.331

Quilici, S., & Rousse, P. (2012). Location of host and host habitat by fruit fly parasitoids. *Insects*, *3*, 1220–1235. https://doi.org/10.3390/insects3041220

Rausher, M. D. (1984). The evolution of habitat preference in subdivided populations. *Evolution*, *38*, 596–608. https://doi.org/10.1111/j.1558-5646.1984.tb00325.x

Schultz, C. B., & Crone, E. E. (2001). Edge-mediated dispersal behavior in a prairie butterfly. *Ecology*, *82*, 1879–1892. https://doi.org/10.1890/0012-9658(2001)082[1879:EMDBIA]2.0.CO;2

Segura, D. F., Hussenbaum, A. L., Viscarret, M. M., Devescovi, F., Bachmann, G. E., Corley, J. C., … Cladera, J. L. (2016). Innate host habitat preference in the parasitoid *Diachasmimorpha longicaudata*: Functional significance and modifications through learning. *PLoS One*, *11*, e0152222. https://doi.org/10.1371/journal.pone.0152222

Shelton, A. M., & Badenes–Perez, F. R. (2006). Concepts and applications of trap cropping in pest management. *Annual Review of Entomology*, *51*, 285–308. https://doi.org/10.1146/annurev.ento.51.110104.150959

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*, 1–12. https://doi.org/10.1186/2051-3933-2-4

Turchin, P. (1991). Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology*, *72*, 1253–1266. https://doi.org/10.2307/1941099

Vet, L. E. M. (1983). Host-habitat location through olfactory cues by *Leptopilina clavipes* (Hartig) (Hym.: Eucoilidae), a parasitoid of fungivorous *Drosophila*: The influence of conditioning. *Netherlands Journal of Zoology*, *33*, 225–248. https://doi.org/10.1163/002829683X00101

Webster, S. E., Galindo, J., Grahame, J. W., & Butlin, R. K. (2012). Habitat choice and speciation. *International Journal of Ecology*, *2012*, Article ID 154686, 12 pp. https://doi.org/10.1155/2012/154686

Zehnder, G. W., & Trumble, J. T. (1984). Host selection of *Liriomyza* species (Diptera: Agromyzidae) and associated parasites in adjacent plantings of tomato and celery. *Environmental Entomology*, *13*, 492–496. https://doi.org/10.1093/ee/13.2.492

Zhao, Y. X., & Kang, L. (2002). The role of plant odours in the leafminer *Liriomyza sativae* (Diptera: Agromyzidae) and its parasitoid *Diglyphus isaea* (Hymenoptera: Eulophidae): Orientation towards the host habitat. *European Journal of Entomology*, *99*, 445–450. https://doi.org/10.14411/eje.2002.056

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